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Review of the subgenus *Larsoceraphron* Dessart, 1981 of the genus *Ceraphron* Jurine, 1807 (Hymenoptera, Ceraphronidae) with the description of a new species from Thailand

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Abstract
The subgenus *Larsoceraphron* Dessart, 1981 of the genus *Ceraphron* Jurine, 1807 is reviewed, and a new species, *Ceraphron* (*Larsoceraphron*) *chularoipaad* **sp. nov.**, from Thailand is described and illustrated. This represents the first species-level record of the genus *Ceraphron* in Thailand. Additionally, we provide the redescriptions and illustrations of three previously known species *viz.*, *C.* (*L.*) *huggerti*, *C.* (*L.*) *sylviae*, and *C.* (*L.*) *tobiasi*. We also include two identification keys for all known subgenera of *Ceraphron* and species of the subgenus *Larsoceraphron*.

Keywords
Identification key, Oriental, redescription, species discovery, Taxonomy

Introduction

The parasitoid wasp superfamily Ceraphronoidea is globally distributed (excluding Antarctica), rather diverse, and frequently collected (Johnson and Musetti 2004; Salden and Peters 2023). This superfamily comprises two extant families, Ceraphronidae

and Megaspilidae, which have been significantly neglected in both morphological and molecular studies (e.g., Salden and Peters 2023). Recently, a review of the Afrotropical fauna of this superfamily was published, more than doubling the number of described species across Africa. Over 80% of the newly described species were collected from a small, threatened forest fragment in Kenya, highlighting how severely understudied this group is and how the current number of described species does not accurately reflect its true diversity (Salden and Peters 2023). Similarly, the situation is mirrored in Southeast Asia, where almost nothing is known about ceraphronoids. There is currently no identification key available for ceraphronoid genera in this region (Butcher and Quicke 2023). The only existing key to genera is that of Dessart and Cancemi (1986), which is a world key and not specific to this region. Moreover, it is outdated, does not reflect current taxonomic advances, and is written in French, further limiting its accessibility and usefulness.

The family Ceraphronidae can be distinguished from Megaspilidae by several characteristics: i) mesotibia with one apical spur, ii) fore wing usually lacking pterostigma (with exceptions like *Trassedia* Cancemi, 1996 and *Masner* Mikó & Deans, 2009), iii) usually lacking notauli, iv) presence of the Waterston's evaporatorium on the sixth tergite, v) first metasomal sternite not subdivided, and vi) simple apex of protibial spur equipped with a comb (Masner and Dessart 1967; Mikó and Deans 2009; Mikó et al. 2018). Genera within Ceraphronidae can be identified using keys provided by Dessart and Cancemi (1986) and Salden and Peters (2023). Despite the severely limited understanding of their biology beyond basic host records, ceraphronids have a wide host range, including Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Thysanoptera, and Trichoptera (e.g., Dessart and Bournier 1971; Luhmann et al. 1999; Hayat et al. 2003; Evans et al. 2005; Matsuo et al. 2016; Moser et al. 2024).

More than 90% of ceraphronid species are classified into two genera, *Ceraphron* Jurine, 1807 (n = 230) and *Aphanogmus* Thomson, 1858 (n = 140), yet many species remain undescribed (Johnson and Musetti 2004; Salden and Peters 2023). However, genus-level identification of female ceraphronids can be challenging with the sole diagnostic character, the width-to-height ratio of the mesosoma (higher than wide in *Aphanogmus* and wider than high in *Ceraphron*) (Ulmer et al. 2018). Ceraphronid wasps are considered a morphologically monotonous group (Mikó et al. 2013). However, ceraphronids from tropical regions might indicate a potentially greater heterogeneity than usually assumed. In particular, some tropical species of *Ceraphron* were found to have well-developed notauli, a character previously considered characteristic for the family Megaspilidae. These findings prompted Dessart (1981) to revise the classification within *Ceraphron*. *Ceraphron* is further divided into six subgenera, all of which were revised by Dessart (1981) and Dessart and Cancemi (1986), including *Allomicrops* Kieffer, 1914 (n = 6), *Ceraphron* (n > 200), *Eulagynodes* Girault, 1917 (n = 9), *Larsoceraphron* Dessart, 1981 (n = 3), *Oktoceraphron* Dessart & Cancemi, 1986 (n = 1), and *Pristomicrops* Kieffer, 1906 (n = 6). The subgenera of *Ceraphron*, apart from the most speciose

subgenus *Ceraphron*, are defined by distinct morphological features. Most species belonging to these morphologically distinct subgenera are found in tropical regions (Afrotropical, Neotropical, and Oriental). However, some subgenera, such as *Allomicrops*, *Eulagynodes*, and *Pristomicrops*, also occur in non-tropical regions. So far, only the monotypic subgenus *Oktoceraphron* and the species of *Larsoceraphron* are known exclusively from tropical habitats. Recent taxonomic literature on the Oriental fauna mostly consists of descriptions of single species within these subgenera (Dessart 1975a, 1981). The present study highlights the necessity and feasibility of focusing on subgenera within *Ceraphron*.

Larsoceraphron is documented in Brazil, Malaysia, and Vietnam (Dessart 1981; Alekseev 2004) and currently lacks biological, ecological, and molecular data. This study provides diagnoses, descriptions, and redescriptions of the subgenus, including the description of a new species, as well as two identification keys: one for the subgenera of *Ceraphron* and another for the species of *Larsoceraphron*. It represents the first confirmed species-level record of the genus *Ceraphron* in Thailand, although the first genus-level record *Ceraphron* (*Allomicrops*), was previously given by Butcher and Quicke (2023).

Material and methods

The terminology of morphological characters follows Mikó and Deans (2009), the Hymenoptera Anatomy Ontology (HAO) (Yoder et al. 2010), Mikó et al. (2013), Ulmer et al. (2018), Trietsch et al. (2020), and Salden and Peters (2023). Specimen preparation, labeling, and photographic plate preparation comply with the methods described by Ghafouri Moghaddam et al. (2017, 2018, 2019). Photographs were captured using a Leica® M205C microscope equipped with montage multi-focus, interactive measurement, and fusion optics stereomicroscope combined with Leica Application Suite. High-resolution images of types from previously described species were examined in this study without direct access to the physical specimens. All images were processed using Adobe Photoshop® CC 2019 software (Adobe Co., San José, CA, USA). The list of depositories is below:

ANIC	Australian National Insect Collection, Canberra, Australia
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada
CUMZ	Chulalongkorn University Museum of Zoology, Bangkok, Thailand
MCSN	Museo Civico di Storia Naturale, Genoa, Italy
MHNG	Muséum d'Histoire Naturelle, Genèva, Switzerland
NHMUK	Natural History Museum, London, United Kingdom
QSBG	Queen Sirikit Botanic Garden, Chang Mai, Thailand
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium

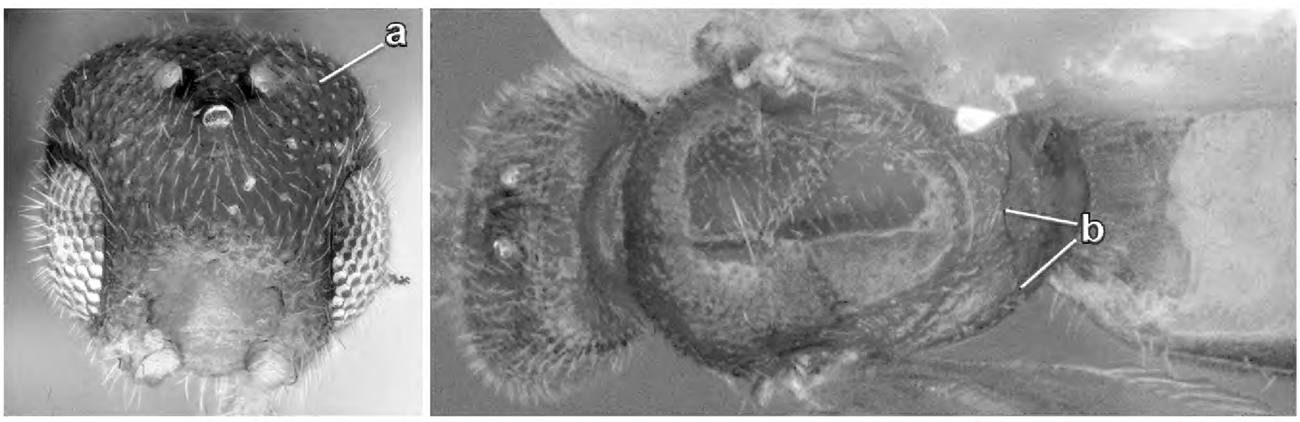
RMCA	Royal Museum for Central Africa, Tervuren, Belgium
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia
ZMUC	Zoological Museum, University of Copenhagen, Denmark
ZMUM	Zoological Museum of Moscow University, Russia

In the case of the new species, one hind leg was removed, allowing for the preservation of the majority of the body. The DNA extraction was carried out in accordance with standard procedures for 96-well plates (Ivanova et al. 2006). The polymerase chain reaction (PCR) amplification and DNA sequencing were performed according to standard protocols (Hajibabaei et al. 2005). The Cytochrome *c* oxidase subunit I (*COI*) fragments were amplified using the LepF1 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and the LepR1 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') primers (Hebert et al. 2003). However, this protocol was unsuccessful, and we were unable to obtain *COI* sequences for the new species.

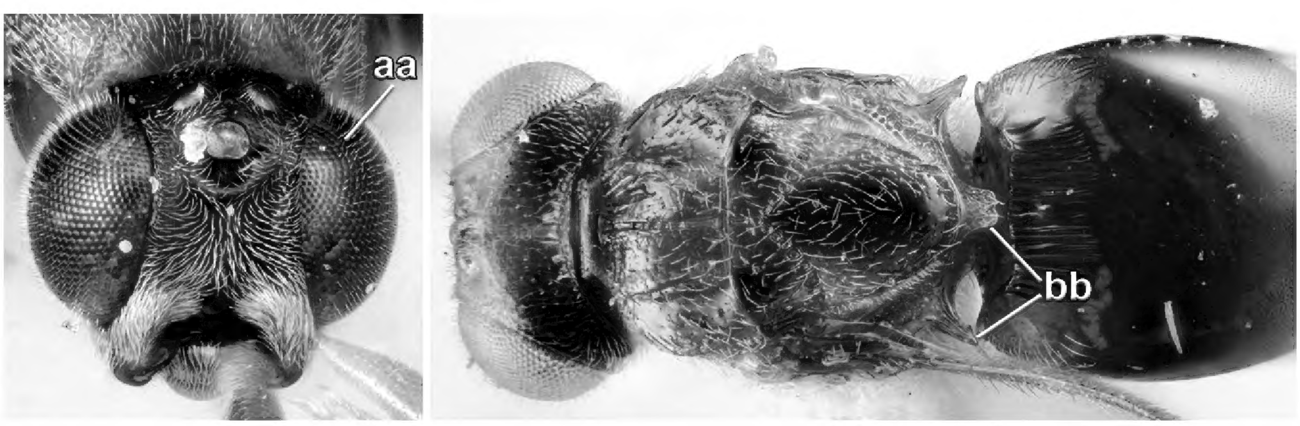
Results

Key to subgenera of *Ceraphron* (modified from Dessart and Cancemi 1986)

1 Head rectangular in frontal view and slightly antero-posteriorly compressed (a); lateral and median propodeal projections absent (b) **2**

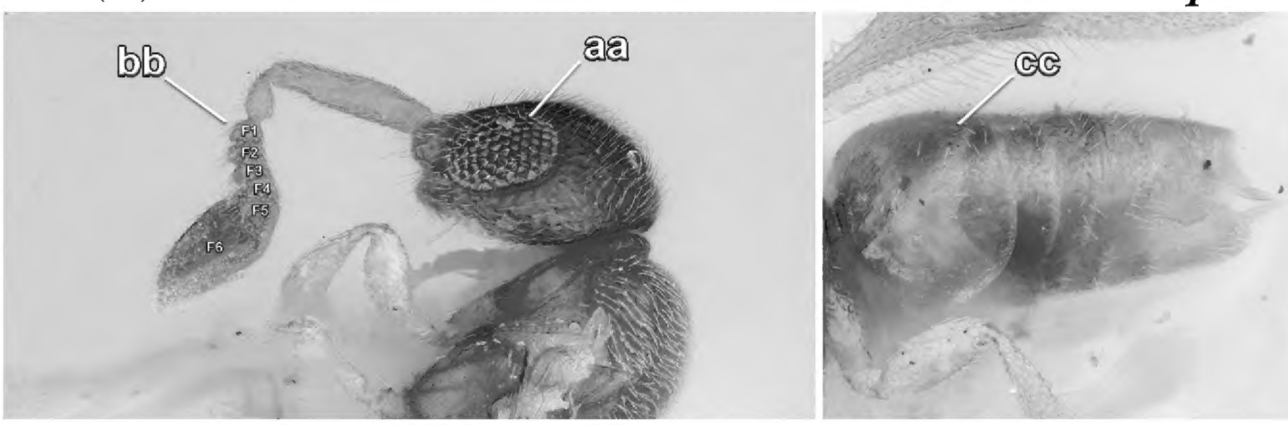


– Head rounded, not rectangular in frontal view (aa); lateral and median propodeal projections present (bb) **3**

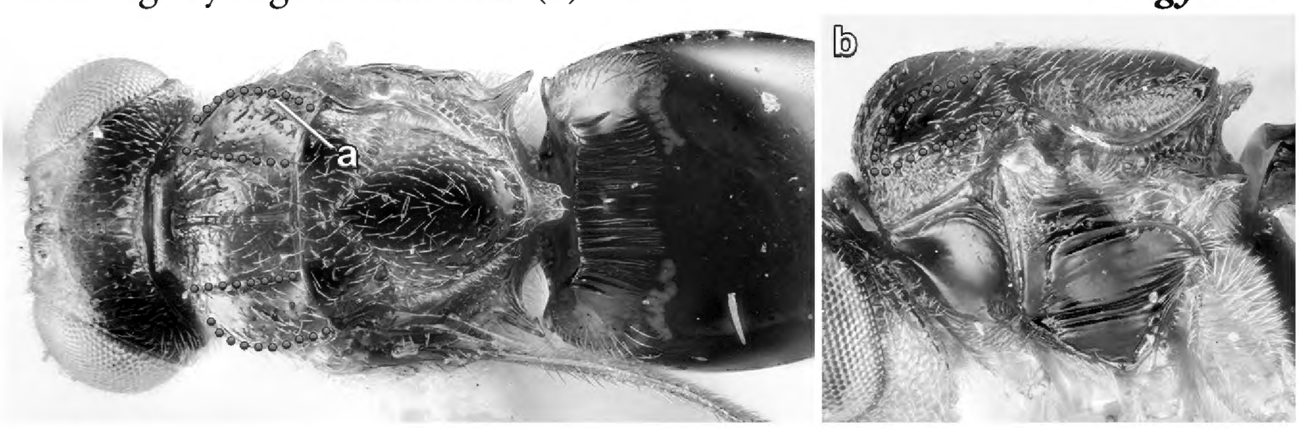


2 Eyes small (a); antenna with eight flagellomeres in females (b); length *vs.* height of syntergite in lateral view at least 0.80 or more (c).....***Pristomicrops***

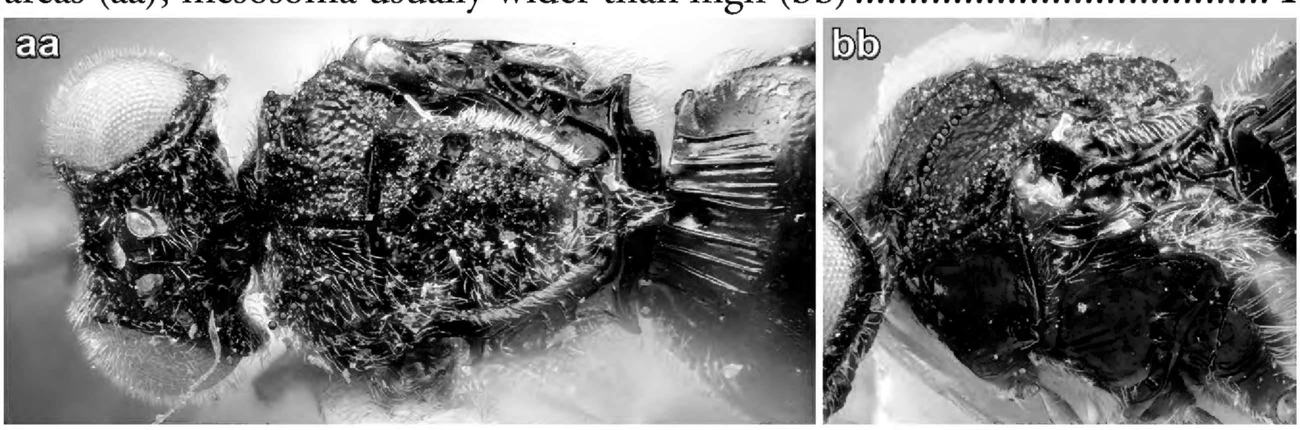
– Eyes medium-sized (aa); antenna with six flagellomeres in female (male unknown) (bb); length *vs.* height of syntergite in lateral view less than 0.60 (cc) .... ***Oktoceraphron***



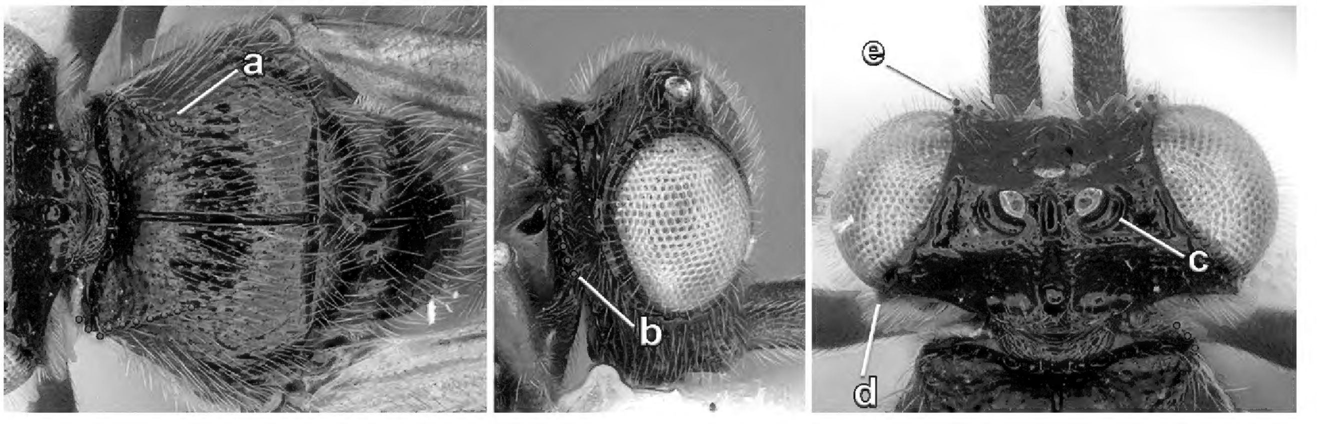
3 Mesoscutum with adnotaular signa (red dotted line) next to notauli (yellow dotted line), dividing the mesoscutum into six longitudinal areas (a); mesosoma slightly higher than wide (b) ....***Eulagynodes***



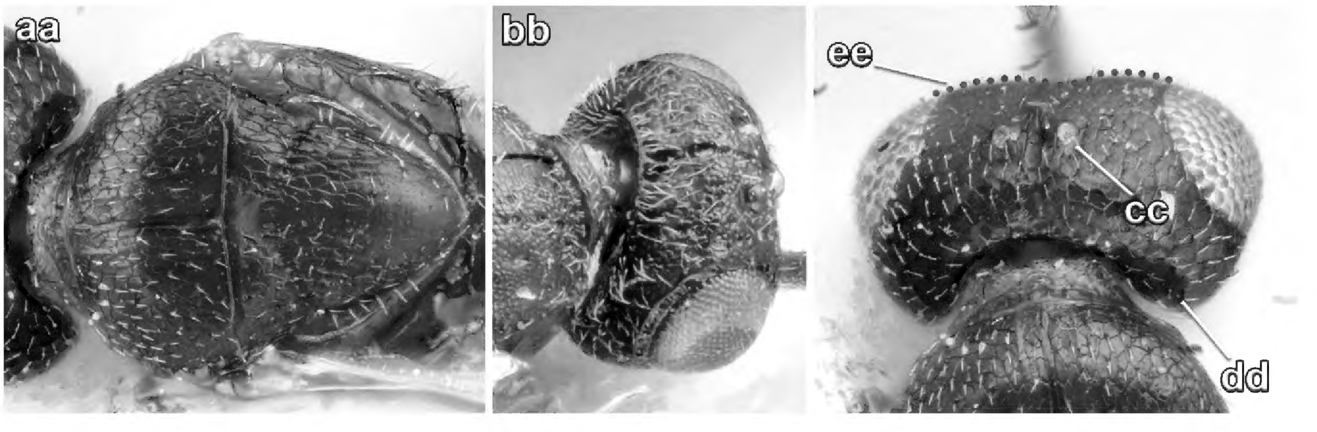
– Mesoscutum at most with median mesoscutal sulcus and notauli, adnotaular signa not complete and not dividing the mesoscutum into six longitudinal areas (aa); mesosoma usually wider than high (bb) **4**



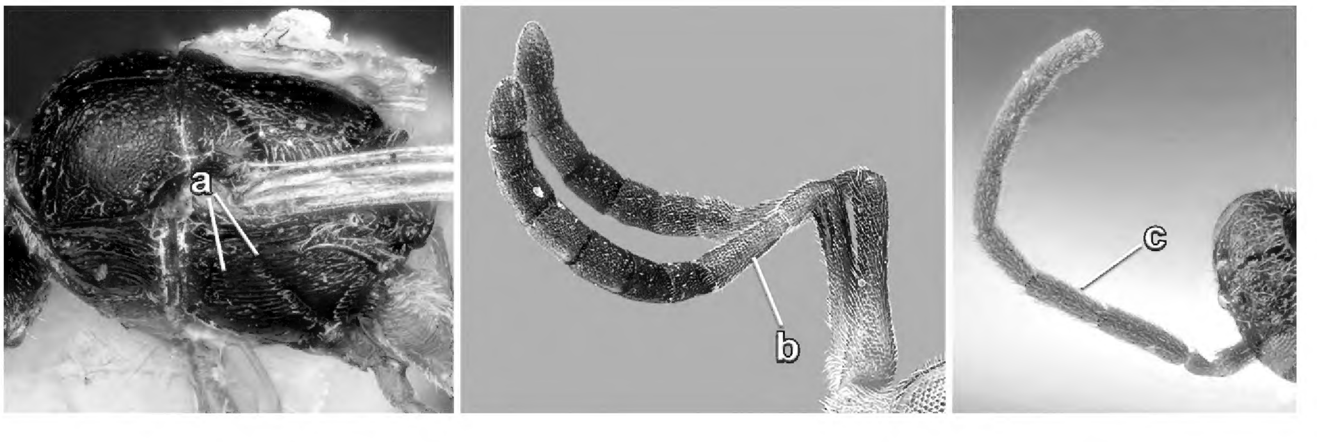
4 Notauli distinct anteriorly and internotaular area distinctly more prominent relative to the scapula (a, yellow dotted line); epomial carina distinct (b, green dotted line); ocellar foveae large (c); occipital carina with lateral part distinctly protruding posteriorly (d); anterior margin of head concave in dorsal view (e, blue dotted line) .... ***Larsoceraphron***



– Notauli usually absent, if present, the internotaular area not more prominent relative to the scapula (aa); epomial carina usually indistinct (bb); ocellar foveae small or absent (cc); occipital carina with lateral part slightly protruding posteriorly or not protruding (dd); anterior margin of head usually less concave in dorsal view (ee) **5**



5 Mesometapleuron with distinct foveolate mesometapleural sulcus and distinct longitudinal striations in dorsal three quarters (a); first flagellomere usually distinctly longer than pedicel in females (b); all flagellomeres distinctly elongated with second flagellomere at least twice as long as wide in males (c) .... ***Allomicrops***



– Without the above combination of characters, different from those in the subgenera mentioned above .... ***Ceraphron sensu stricto***

Key to species of the subgenus *Larsoceraphron*

1 Malar distance short (Fig. 2C); anterior ocellar fovea triangular with carinate margins and anterior end slightly pointed upwards (Fig. 2C, E); notauli complete (Fig. 2F) .... ***C.* (*L.*) *huggerti* Dessart, 1981**

– Malar distance elongate (Figs 1C, 4C); anterior ocellar fovea not triangular (Figs 1C, E, 4C, E, 5E); notauli incomplete (Figs 1F, 4F, 5F) **2**

2 Mesosoma and metasoma reddish-brown with the anterior mesoscutum, anterolateral axillae, ventral mesopleuron, synsternite, and syntergite partially black (Figs 4A, F–J, 5A, F–J); lateral margins of toruli extremely raised (Fig. 4C, E); notauli distinctly broadened (Figs 4F, 5F).. .... ***C.* (*L.*) *sylviae* Dessart, 1981**

– Mesosoma and metasoma dark brown or black, not reddish-brown (Fig. 1A, F–K); lateral margins of toruli less distinctly raised (Fig. 1C, E); notauli not distinctly broadened (Fig. 1F) **3**

3 Eyes very large; 5th flagellomere yellowish-brown; scape slightly shorter than the pedicel and 1st to 4th flagellomere combined (Fig. 6H); mesometapleuron with longitudinal striation in ventral two thirds; metafemur distinctly thickened, length slightly more than 2.0 × its maximum width .... ***C.* (*L.*) *tobiasi* Alekseev, 2004**

– Eyes medium-sized (Fig. 1C–E); 5th flagellomere dark brown (Fig. 1A); scape 1.23 × the pedicel and 1st to 4th flagellomere combined (Fig. 1A); mesometapleuron with longitudinal striation in dorsal two thirds (Fig. 1I); metafemur slightly thickened, length 3.8 × its maximum width (Fig. 1A)...................... .... ***C.* (*L.*) *chularoipaad* sp. nov.**

Taxonomic accounts

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Superfamily Ceraphronoidea Haliday, 1833
Family Ceraphronidae Haliday, 1833
Genus *Ceraphron* Jurine, 1807

Subgenus *Larsoceraphron* Dessart, 1981

Type species. *Ceraphron* (*Larsoceraphron*) *sylviae* Dessart, 1981 by original designation.

Type information. Holotype female, CNC. Country of type locality: Brazil.

Diagnosis. *Larsoceraphron* is distinguished from all other subgenera of *Ceraphron* by the following combination of characters: lateral ocelli separated by a wide and foveolate occipital furrow, and laterally and posteriorly surrounded by distinctly large ocellar foveae (Figs 1C, E, 2C, E, 4C, E, 5E, 6A); median ocellus with distinctly large and ventrally extended ocellar fovea (Figs 1C, E, 2C, E, 4C, E, 5E, 6A); anterior margin of head concave in dorsal view (Figs 1E, 2E,

4E, 5E, 6A); distinct occipital carina with lateral part distinctly protruding posteriorly (Figs 1E, 2E, 4E, 5E, 6A); head and mesosoma with randomly sized areolae and strongly sculptured (Figs 1C–G, I, 2C–G, I, 4C–F, I, 5D–F, I, 6A, B); epomial carina distinct (Figs 1E, F, 2E, 4E, 5E, 6A); notauli distinct at least in anterior third and internotaular area distinctly more prominent relative to the scapula (Figs 1F, 2F, 4F, 5F, 6A).

Number of species. Four species are known, including the newly described species.

Biology. Unknown.

Molecular data. Unknown.

Geographical distribution. Neotropical: Brazil (Dessart 1981); Oriental: Malaysia (Dessart 1981), Vietnam (Alekseev 2004), Thailand (present study).

***Ceraphron* (*Larsoceraphron*) *chularoipaad* Ghafouri Moghaddam, Salden & Butcher, sp. nov.**

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Fig. 1A–K

Type material examined. ***Holotype*** • female, THAILAND, Nan, Pua, Phu Kha, Doi Phu Kha National Park 1, 19°12.236'N, 101°04.667'E, 1341 m, hill Evergreen Forest, Malaise trap, Global Malaise Program, 19.viii.2023, B. A. Butcher leg., MGM0388 and BBTH6665–24 (for DNA Barcoding), CUMZ-HYM00393, CUMZ. ***Paratype*** • female, THAILAND, Chiang Mai, Fang, Pong Nam Ron, Doi Pha Hom Pok National Park, Kiew Lom viewpoint, 20°3.49'N, 99°8.552'E, 2174 m, Malaise trap, 14–21.xi.2007, P. Wongchai leg., T6203, QSBG.

Diagnosis. Eyes medium-sized (Fig. 1C, D); anterior ocellar fovea ventrally extended into facial sulcus, reaching dorsal margin of antennal scrobe (Fig. 1C, E); occipital carina straight (Fig. 1D, E); slightly elongated areolae between eyes and ocellar foveae of lateral ocelli (Fig. 1C, E); scape 1.23 × the pedicel and 1st to 4th flagellomere combined (Fig. 1A); notauli present in anterior one third (Fig. 1F); mesoscutum and -scutellum with no distinct areolae (Fig. 1F, G); metafemur slightly thickened, length 3.8 × its maximum width (Fig. 1A); basal longitudinal carinae on the syntergite covering half of the width of the anterior syntergite (Fig. 1G, H).

Description (Female). Body length 2.6 mm.

Colour. Head and mesosoma black, coxae black to dark brown (Fig. 1A, C–G); metasoma, apex of scape, pedicel, and thickened four apical flagellomeres dark brown, base of scape, other flagellomeres, and legs brown (Fig. 1A, J, K); palpi yellow (Fig. 1A); fore wing disc slightly infuscated, hind wings virtually transparent (Fig. 1B); wing venation light brown (Fig. 1B).

Head. Slightly longitudinal in frontal view with medium long malar distance (Fig. 1C); lateral margin of toruli raised; width of the head slightly wider than the maximum width of the mesosoma, densely pubescent (Fig. 1A, I); eyes medium-sized, covered with erect setae (Fig. 1C–E); slightly crenulate ocular impressions

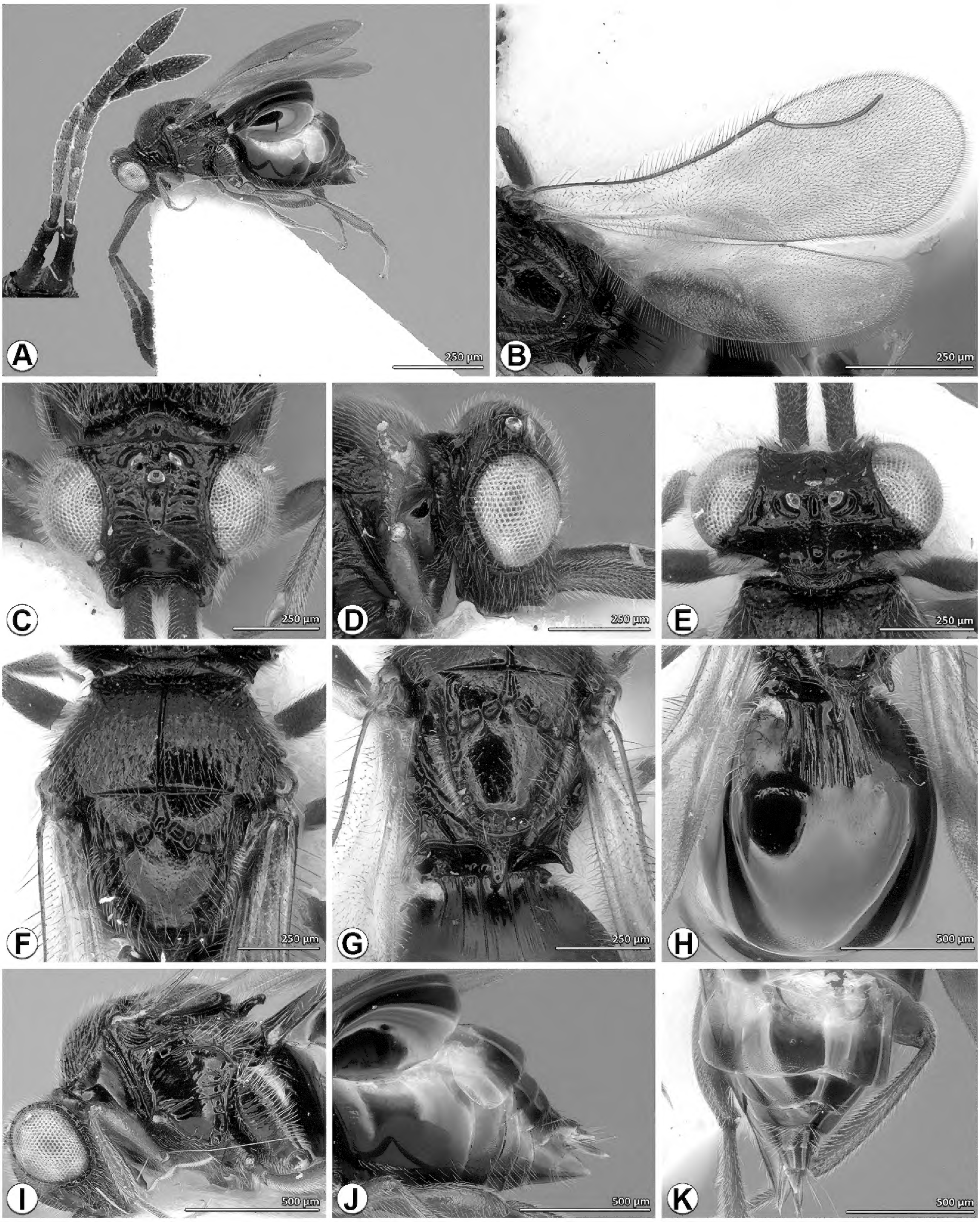

Figure 1. *Ceraphron* (*Larsoceraphron*) *chularoipaad* sp. nov., female holotype from Thailand (CUMZ) **A** habitus and antenna, lateral view **B** fore and hind wing **C** head, dorsofrontal view **D** head, lateral view **E** head, dorsal view **F** mesosoma, dorsal view **G** posterior mesosoma and anterior syntergum, dorsal view **H** syntergum, dorsal view **I** head and mesosoma, lateral view **J** metasoma, lateral view **K** posterior metasoma, dorsal view.

along the inner margin of the eye (Fig. 1C, E); slightly elongated areolae between eyes and ocellar foveae of lateral ocelli (Fig. 1C, E); median ocellus diameter 1.2 × LOL (lateral ocellar line) (Fig. 1C, E); occipital carina straight, with lateral part

slightly posteriorly protruding (Fig. 1D, E); anterior ocellar fovea elongated and ventrally extended into facial sulcus, reaching dorsal margin of antennal scrobe (Fig. 1C, E); intertorular sclerite and clypeus with pubescence (Fig. 1C); interocular distance 0.4 × head width (Fig. 1C); antennae with four apical flagellomeres distinctly thickened (Fig. 1A); scape 1.23 × the pedicel and 1st to 4th flagellomere combined (Fig. 1A); pedicel about equal to the length of the 1st flagellomere (Fig. 1A); 4th and 5th flagellomeres about equal in length and width, width of 4th flagellomere 1.11, and 5th 1.26 × their length, respectively (Fig. 1A); the 6th–8th flagellomeres not transverse, width of 6th flagellomere 0.78, 7th 0.69, and 8th 0.38 × their length, respectively (Fig. 1A).

Mesosoma. Mesoscutum transverse, width 2.0 × its length (from dorsal view) (Fig. 1F); notauli incomplete, present in anterior one third (Fig. 1F); mesoscutum and -scutellum with no distinct areolae (Fig. 1G); scutoscutellar sulci converge medially, adjacent to transscutal articulation (Fig. 1G); mesometapleuron with longitudinal striations in dorsal two thirds, smooth in ventral one third (Fig. 1I); lateral propodeal projections distinctly long and oriented posteriorly, tip of the projections amber-coloured (Fig. 1G, H); median propodeal projection overhangs the anterior margin of the metasoma with its apical half, with slightly rounded tip from dorsal view (Fig. 1G, H).

Legs. Metacoxa with few longitudinal striations (Fig. 1A, I); metafemur slightly thickened, length 3.8 × its maximum width (Fig. 1A).

Metasoma. Six basal longitudinal carinae on the syntergite covering half of the width of the anterior syntergite (Fig. 1G, H); anterolateral syntergite with row of setae as long as basal longitudinal carina (Fig. 1J, K).

Male. Unknown.

Host. Unknown.

Distribution. Oriental (Thailand).

Etymology. The specific epithet *chularoipaad* is derived from “Chula”, referring to Chulalongkorn University, and “roi paad”, which means “one hundred and eight” in Thai, commemorating the 108th anniversary of Chulalongkorn University in 2025. The name is treated as a noun in apposition.

Ceraphron (*Larsoceraphron*) *huggerti* Dessart, 1981

Figs 2A–K, 3A, B, 6A–E

Type material examined. ***Holotype*** • male, Malaysia, Sarawak, first division, about 20 km South of Kuching, Semenggoh Nature Reserve, 28–30.ix.1979, M. Söderlund leg., préparation microscopique n° 8011/281, PSUC_FEM 000147213, RBINS (Fig. 2K).

Diagnosis. Antennae brown with last five flagellomeres dark brown (Fig. 2A, B); head transverse in frontal view with short malar distance (Fig. 2C); anterior ocellar fovea ventrally slightly extended, triangular with carinate margins and anterior end slightly pointed upwards (Fig. 2C, E); mesoscutum colliculate (Fig. 2F); mesoscutum strongly transverse, width 3.5 × its length (Fig. 2F, I); notauli complete (Fig. 2F);

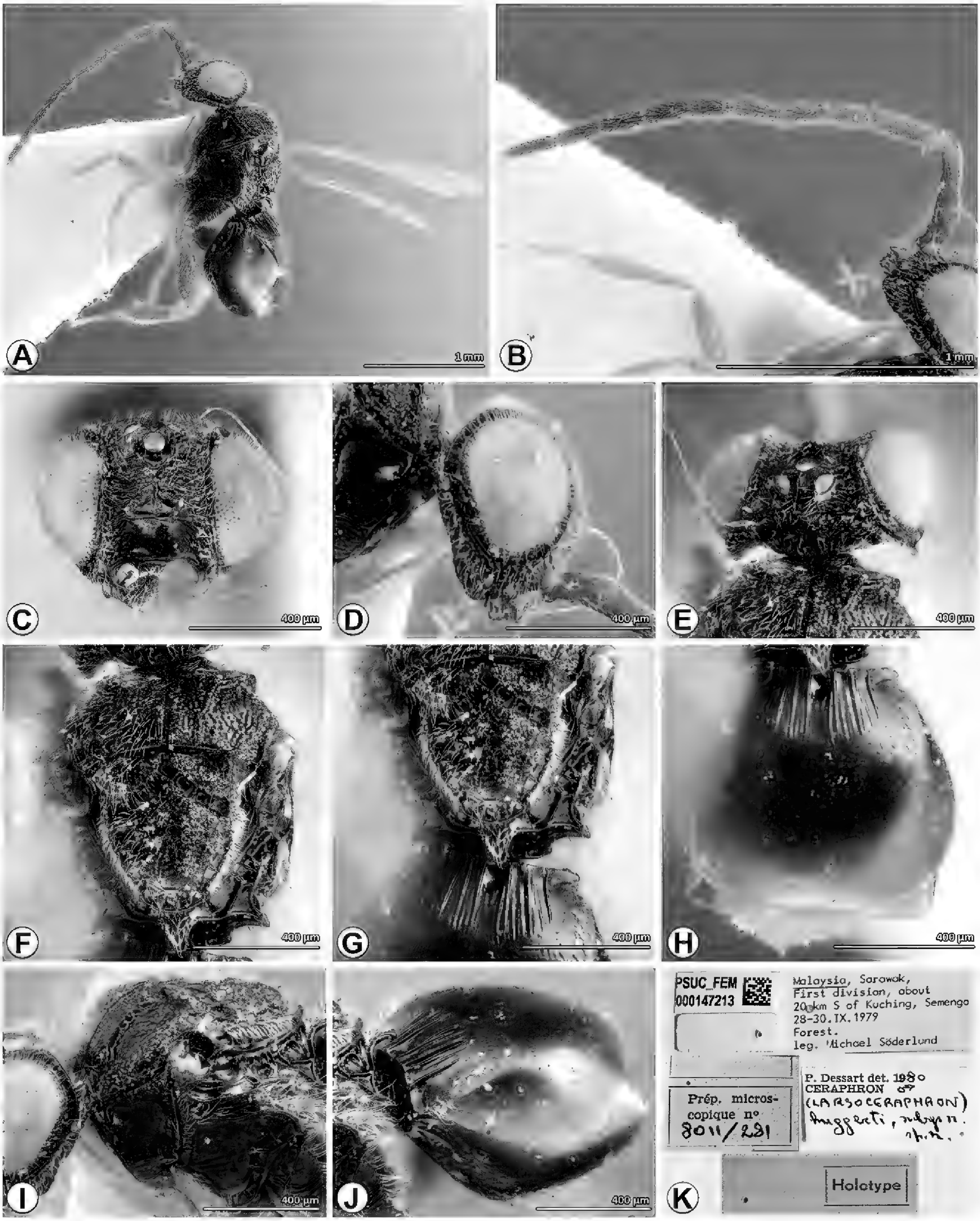

Figure 2. *Ceraphron* (*Larsoceraphron*) *huggerti*, male holotype from Malaysia (RBINS) **A** habitus, lateral view **B** left antenna **C** head, frontal view **D** head, lateral view **E** head, dorsal view **F** mesosoma, dorsal view **G** posterior mesosoma and anterior syntergum, dorsal view **H** metasoma, dorsal view **I** mesosoma, lateral view **J** metasoma, lateral view **K** original labels.

mesometapleuron smooth with small and few incomplete striations (Fig. 2I); median propodeal projection with rectangular tip from dorsal view (Fig. 2); distinct pit posteromedially of the basal transverse carina on the syntergite (Fig. 2H, J); harpe/gvc

index 0.76, harpe with at least two apical setae, longest apical setae of harpe 1.3 × as long as harpe; harpe with at least five median setae (Figs 3A, B, 6C).

Re-description (male). Body length 2.7 mm.

Colour. Head and mesosoma black (Fig. 2A, C–G, I), metasoma dark brown (Fig. 2A, H, J); antennae brown with last five flagellomeres dark brown (Fig. 2A, B); coxae black, the rest of the legs dark brown (Fig. 2A); fore wing disc infuscated, hind wing disc slightly infuscated; wing venation brown.

Head. Transverse in frontal view with short malar distance (Figs 2C, 6A); lateral margin of toruli raised; width of the head equal to width of the mesosoma (Figs 2A, 6A); densely pubescence (Fig. 2C–E); eyes large, covered with erect setae (Fig. 2C–E); slightly crenulate ocular impressions along the inner margin of the eye (Fig. 2C, E); dorsal head with randomly sized areolae (Figs 2D, 6A); median ocellus diameter 1.5 × LOL (Figs 2E, 6A); occipital carina distinctly concave, with lateral part posteriorly protruding (Figs 2D, E, 6A); anterior ocellar fovea ventrally slightly extended, triangular with carinate margins and anterior end slightly pointed upwards (Figs 2E, 6A); facial sulcus ends at transverse line, dorsally adjacent to the smooth supraclypeal depression (Fig. 2C); interocular sclerite and clypeus with pubescence (Fig. 2C); interocular distance 0.45 × head width (Fig. 2C); scape almost 4.0 × as long as wide (Figs 2B, 6A, E); moderately elongated cylindrical flagellomeres (Figs 2B, 6E).

Mesosoma. Mesoscutum colliculate, strongly transverse, width 3.5 × its length and anteriorly distinctly steep (Figs 2F, I, 6B); notauli complete and less distinct in posterior part (Figs 2F, I, 6A); mesoscutum with no randomly sized areolae, mesoscutellum with large randomly sized areolae (Figs 2F, G, 6A); scutoscutellar sulci converge medially, adjacent to transscutal articulation (Figs 2F, 6A); mesometapleuron smooth

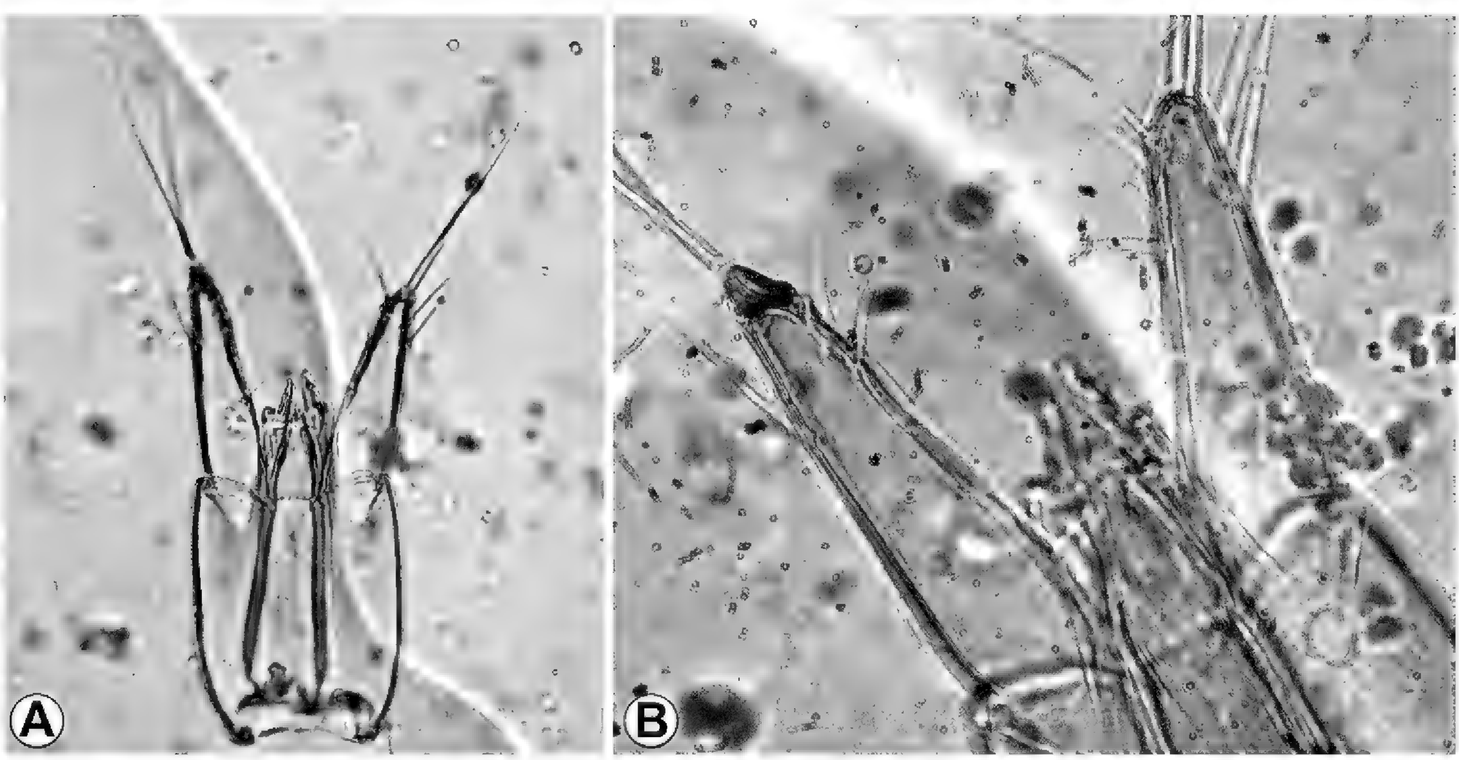

Figure 3. *Ceraphron* (*Larsoceraphron*) *huggerti*, male genitalia holotype from Malaysia (RBINS) **A** ventral view **B** harpes and aedeagus. For the full list of male genitalia characters, see Salden and Peters (2023).

with small and few incomplete striations (Figs 2I, 6B); lateral propodeal projections medium-sized and oriented posterolaterally, pointed tip of the projections amber-coloured (Figs 2G, 6A); median propodeal projection overhangs the anterior margin of the metasoma with its apical half, with rectangular tip from dorsal view (Figs 2G, 6A).

Legs. Metacoxa with longitudinal striations (Figs 2A, 6B); metafemur distinctly thickened, length 2.4 × its maximum width (Fig. 2A).

Metasoma. Seven basal longitudinal carinae on the syntergite covering three thirds of the width of the anterior syntergite (Figs 2G, H, J, 6A); distinct pit posteromedially of the basal transverse carina on the syntergite (Figs 2H, I, 6A); anterolateral syntergite with row of setae as long as basal longitudinal carina (Fig. 2I).

Genitalia (n° 8011/281) (Figs 3A, B, 6C). Genitalia length 2.38 × gvc width; gvc width three quarters of gvc length; gvc width 1.09 × distal gvc width. Harpe triangular to cone-shaped; harpe/gvc index 0.76; lateral articulation site of harpe with gvc not flush; lateral margin of harpe straight; medial margins of harpes slightly converging at distodorsal margin of gvc, dorsomedial margin of harpe virtually straight and slightly diverging distolaterally from base to apex, apex of harpe pointed, oriented distolaterally. Harpe with at least two lateral setae restricted to apical quarter, longest lateral setae half as long as harpe; harpe with at least two apical setae, longest apical setae of harpe 1.3 × as long as harpe; harpe with at least five median setae, longest median setae slightly less than half as long as harpe. Aedeagus + gonossiculus more than half as long as harpe, apex of aedeagus + gonossiculus acute.

Body measurements. For further measurements, refer to Dessart (1981).

Female. Unknown.

Host. Unknown.

Distribution. Oriental (Malaysia).

***Ceraphron* (*Larsoceraphron*) *sylviae* Dessart, 1981**

Figs 4A–K, 5A–K, 6F, G

Type material examined. ***Holotype*** • female, Brazil, Mato Grosso, Sinop, xi.1975, Malaise trap, M. Alvarenga leg., préparation microscopique n° 8102/052, CNC (Fig. 4K). ***Allotype*** • male, Brazil, Amazon, Moura, on the Rio Negro, 20.ii.1973, B. V. Peterson leg., préparation microscopique n° 8102/051, CNC (Fig. 5K).

Diagnosis. Mesosoma and metasoma reddish-brown with the anterior mesoscutum (Fig. 4A, F), anterolateral axillae, ventral mesopleuron, synsternite, and syntergite partially black (Fig. 4F, I, G, H); anterior ocellar fovea U-shaped and ventrally extended into facial sulcus (Fig. 4E); lateral margins of toruli extremely raised (Fig. 4C); pedicel 1.2 × longer than the 1st flagellomere (Figs 4A, 6G); width of 4th flagellomere 1.08 × its length (Figs 4A, 6G); notauli distinctly broadened (Fig. 4F); median mesoscutal sulcus broadened (Fig. 4F); mesoscutum and -scutellum equipped with large randomly sized areolae (Fig. 4F); mesometapleuron with distinct longitudinal striations (Fig. 4I).

Re-description (female). Body length 2.7 mm.

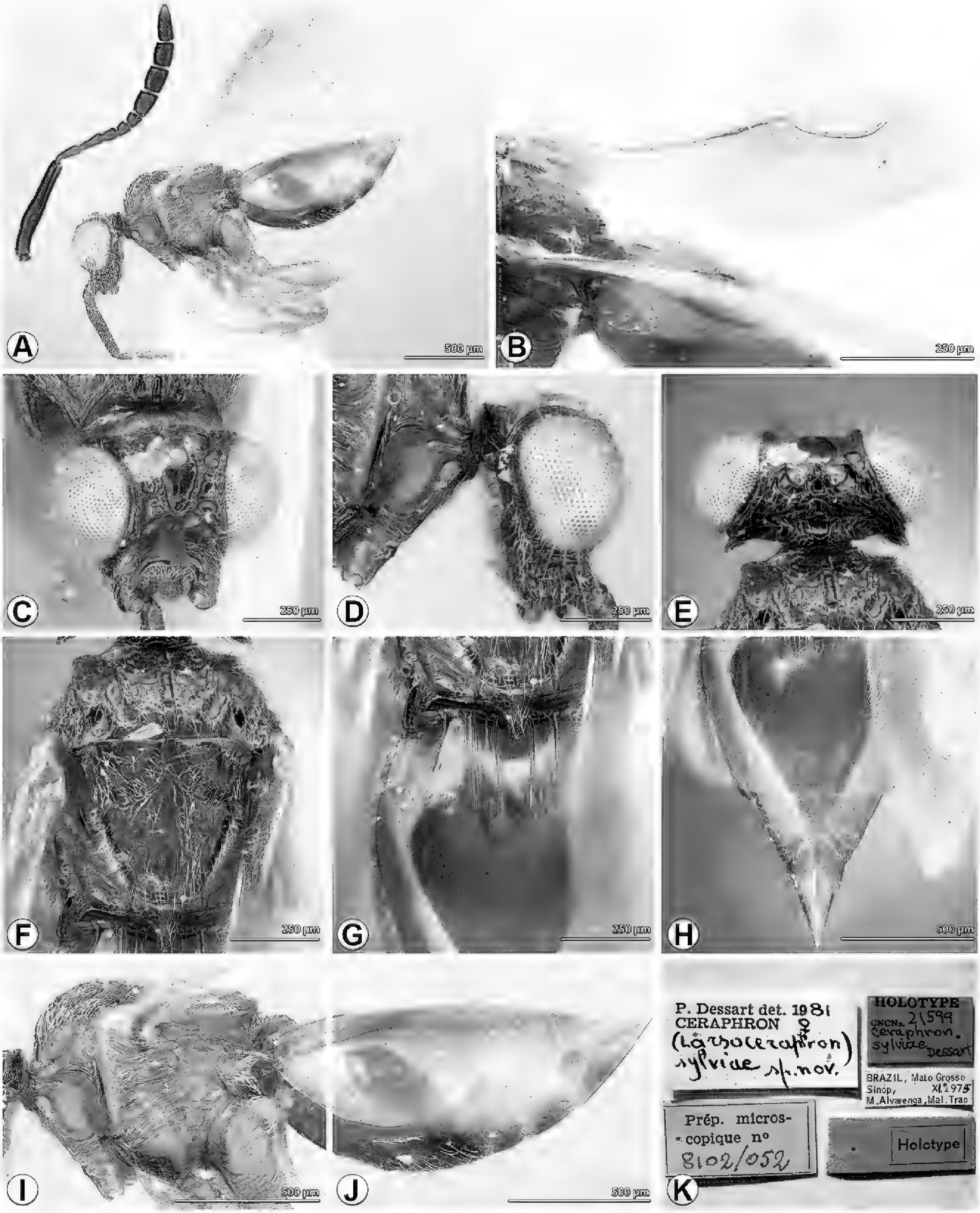

Figure 4. *Ceraphron* (*Larsoceraphron*) *sylviae*, female holotype from Brazil (CNC) **A** habitus and left antenna, lateral view **B** wings **C** head, frontal view **D** head, lateral view **E** head, dorsal view **F** mesosoma, dorsal view **G** posterior mesosoma and syntergum, dorsal view **H** posterior metasoma, dorsal view **I** mesosoma, lateral view **J** metasoma, lateral view **K** original labels.

Colour. Head black, mesosoma and metasoma reddish-brown, with the anterior mesoscutum, anterolateral axillae, ventral mesopleuron, synsternite, and syntergite partially black (Fig. 4A, F–J); antennae dark brown with pedicel and basal five

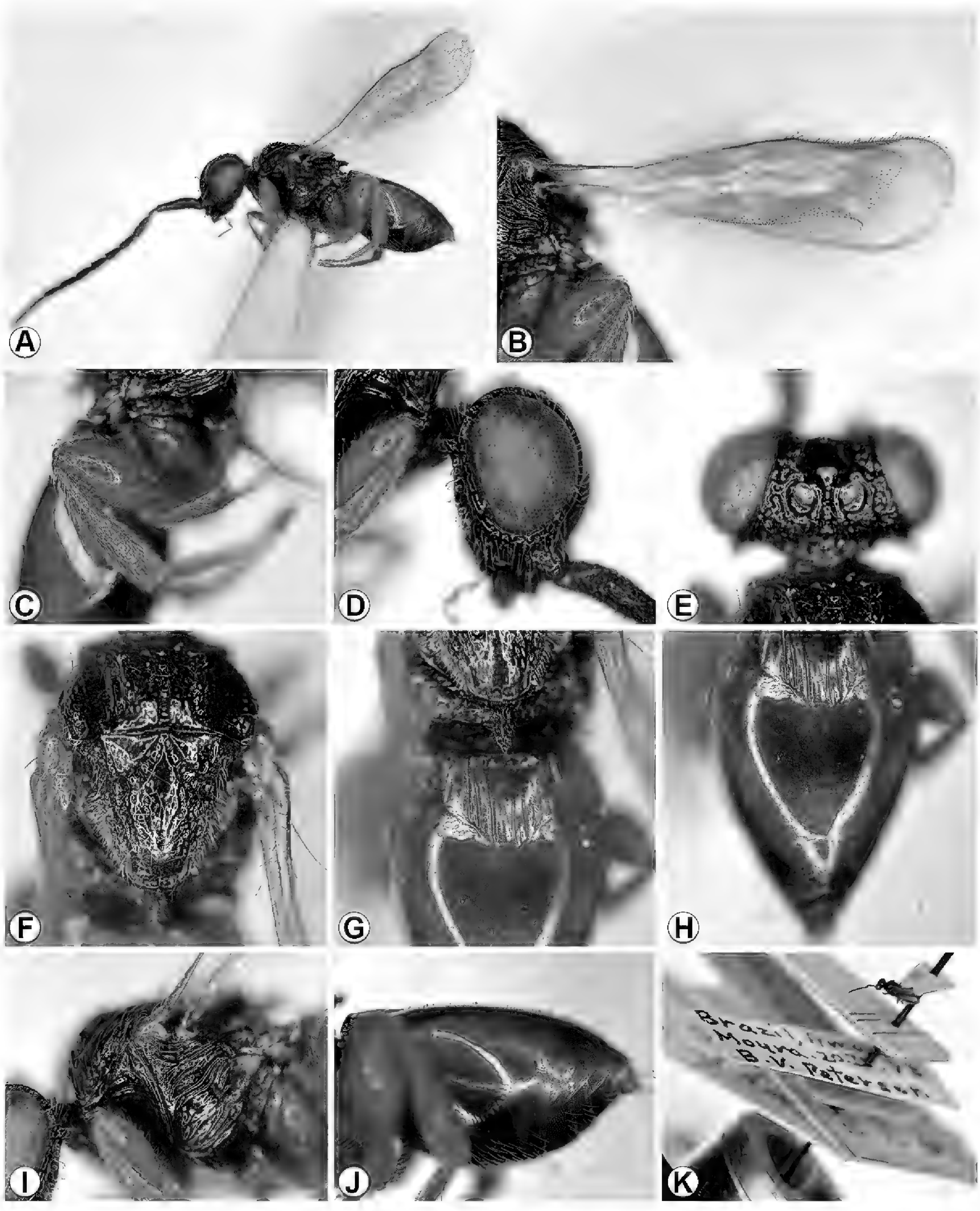

Figure 5. *Ceraphron* (*Larsoceraphron*) *sylviae*, male allotype from Brazil (CNC) **A** habitus and left antenna, lateral view **B** wings **C** hind leg, lateral view **D** head, lateral view **E** head, dorsal view **F** mesosoma, dorsal view **G** posterior mesosoma and syntergum, dorsal view **H** posterior metasoma, dorsal view **I** mesosoma, lateral view **J** metasoma, lateral view **K** original labels.

flagellomeres lighter (Fig. 4A); coxae brown, the rest of the legs yellowish (Fig. 4A); fore wing disc slightly infuscated (Fig. 4B); wing venation light brown (Fig. 4B).

Head. Slightly longitudinal in frontal view with long malar distance, width of the head equal to width of the mesosoma, densely pubescent (Fig. 4C–E); lateral margins of toruli

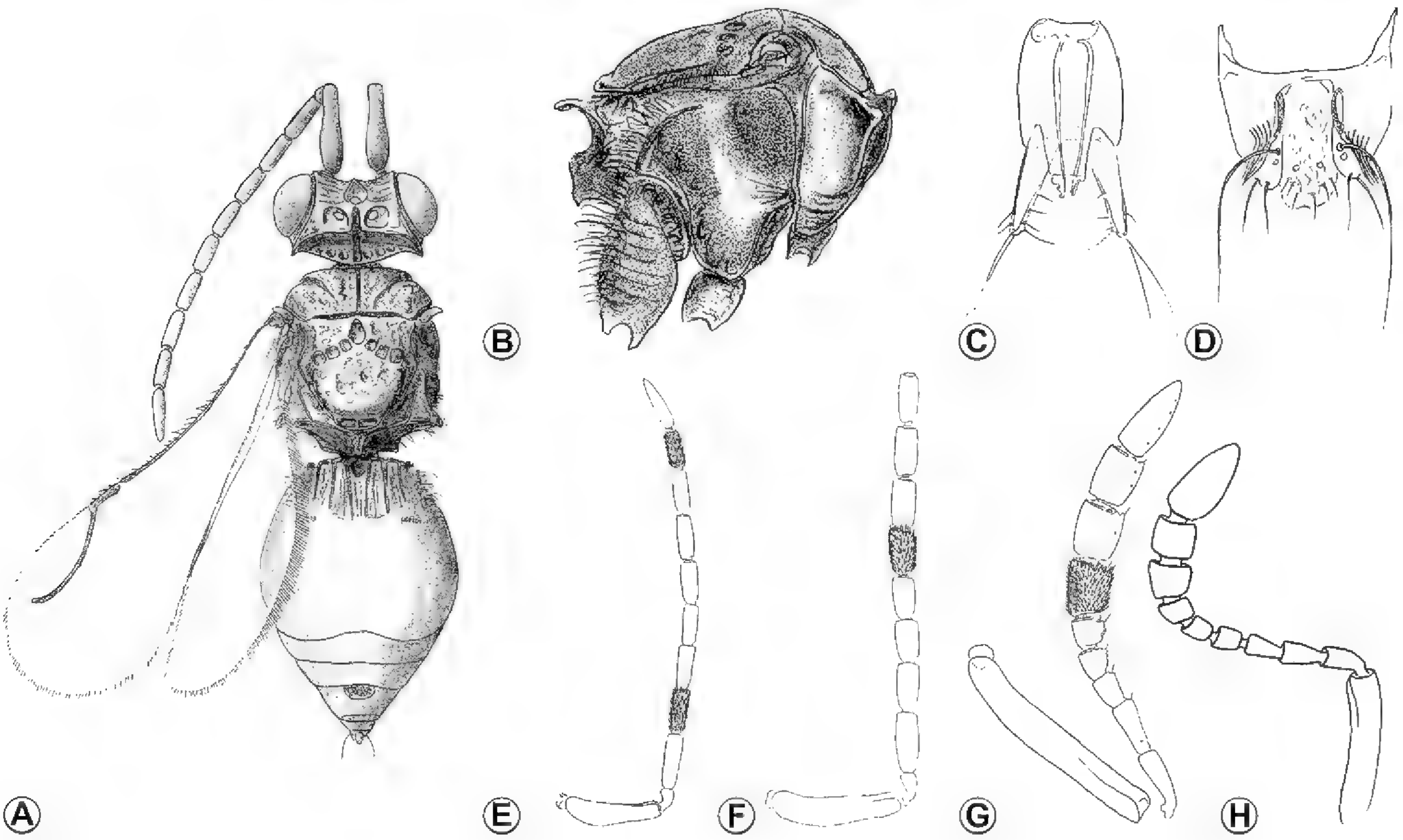

Figure 6. *Ceraphron* (*Larsoceraphron*) spp. (modified drawings from the original descriptions of the species (Dessart 1981; Alekseev 2004)) **A–E** *Ceraphron* (*L.*) *huggerti* **F–G** *Ceraphron* (*L.*) *sylviae* **H** *Ceraphron* (*L.*) *tobiasi* **A** habitus, dorsal view **B** mesosoma, lateral view **C** male genitalia, ventral view **D** tergite 9 and 10, dorsal view **E** antenna (male) **F** antenna (male) **G** antenna (female) **H** antenna (female).

extremely raised; eyes large, covered with erect setae (Fig. 4C–E); slightly crenulate ocular impressions along the inner margin of the eye (Fig. 4C, E); dorsal head with distinct randomly sized areolae (Fig. 4E); median ocellus diameter 1.6 × LOL (Fig. 4E); occipital carina distinctly concave, with lateral part distinctly posteriorly protruding (Fig. 4D, E); anterior ocellar fovea U-shaped and ventrally extended into facial sulcus, almost reaching dorsal margin of antennal scrobe (Fig. 4E); facial sulcus ends at areolae between the facial sulcus and the smooth supraclypeal depression (Fig. 4C); intertorular sclerite and clypeus with distinct pubescence (Fig. 4C); interocular distance 0.43 × head width (Fig. 4C); antennae with four apical flagellomeres distinctly thickened (Figs 4A, 6G); scape 1.10 × the pedicel and 1^{st} to 4^{th} flagellomere combined (Figs 4A, 6G); pedicel 1.2 × longer than the 1^{st} flagellomere (Figs 4A, 6G); width of 4^{th} flagellomere 1.08 × its length (Figs 4A, 6G); width of 5^{th} flagellomere 0.71, 6^{th} 0.75, 7^{th} 0.73, and 8^{th} 0.39 × its length, respectively (Figs 4A, 6G).

Mesosoma. Mesoscutum strongly transverse, width 2.5 × its length and anteriorly distinctly steep (Fig. 4F, I); notauli distinctly broadened, incomplete, almost adjacent to transscutal articulation (Fig. 4F); mesoscutum and -scutellum equipped with large randomly sized areolae (Fig. 4F); scutoscutellar sulci converge medially, adjacent to transscutal articulation (Fig. 4F); mesometapleuron with distinct longitudinal striations, smooth in ventral one quarter (Fig. 4I); lateral propodeal projections distinctly long and oriented posteriorly, reddish-brown (Fig. 4G); median propodeal projection overhangs the anterior margin of the metasoma with its apical half, with slightly rounded tip from dorsal view (Fig. 4G).

Legs. Metacoxa with several longitudinal striations (Fig. 4A, I); metafemur distinctly thickened, length 2.8 × its maximum width (Fig. 4A).

Metasoma. Six basal longitudinal carinae on the syntergite covering three quarters of the width of the anterior syntergite (Fig. 4G); anterolateral syntergite with row of setae slightly shorter than basal longitudinal carinae (Fig. 4 H).

Body measurements. For further measurements, refer to Dessart (1981).

Re-description (male). Body length 2.7 mm.

Apart from the sex specific characters like the shape of the flagellomeres and genitalia/terminalia structure, the male differs from the female in the following:

The mesosoma is black like the head (Fig. 5A, F, I); the head, mesoscutum, and -scutellum are equipped with less distinct areolae (Fig. 5D–F); the lateral margins of the toruli are less raised and the lateral part of the occipital carina is distinctly less protruding posteriorly (Fig. 5D, E); the mesometapleural sulcus is slightly indicated (Fig. 5I); the width of the head is slightly wider than the width of the mesosoma (Fig. 5A).

Body measurements. For further measurements, refer to Dessart (1981).

Host. Unknown.

Distribution. Neotropical (Brazil).

Remarks. The male specimen of *C. sylviae* can be separated from *C. huggerti* by its presence of a mesometapleural sulcus. Male genitalia of both species could not be compared but need future revision.

Ceraphron **(*Larsoceraphron*)** ***tobiasi*** **Alekseev, 2004**

Fig. 6H

Type material (not examined but original description checked). ***Holotype*** • female, Vietnam, Tam Dao, pr. Vĩnh Phúc (= Vinh Phuc), 21°21'N, 105°38'E, 700 m, pines, 14.xi.1990, S. Belokobylskij leg., ZIN.

Diagnosis. The last three flagellomeres dark brown; lateral part of occipital carina almost not posteriorly protruding; interocular distance 0.3 × head width; scape slightly shorter than the pedicel and 1st to 4th flagellomere combined (Fig. 6H); scutoscutellar sulci converge medially, not adjacent to transscutal articulation; mesometapleuron with longitudinal striations in ventral two thirds, smooth in dorsal one third.

Reinterpreted description (female). Body length 2.3–2.4 mm.

Colour. Head, mesosoma, and coxae black; metasoma, apex of scape, pedicel, and the last three flagellomeres dark brown, the rest of the antenna and legs brown or yellowish-brown; fore wing disc slightly infuscated, hind wing disc transparent.

Head. Width of the head slightly wider than width of the mesosoma; densely pubescent; eyes very large, covered with erect setae; crenulate ocular impressions along the inner margin of the eye; lateral part of occipital carina almost not posteriorly protruding; interocular distance 0.3 × head width; antennae with four apical flagellomeres distinctly thickened (Fig. 6H); scape slightly shorter than the pedicel and 1st to 4th flagellomere combined (Fig. 6H); pedicel about equal to the length of the 1st flagellomere

(Fig. 6H); 3th and 4th flagellomeres about equal in length and width (Fig. 6H); 5th–7th flagellomeres transverse, width of the 5th flagellomere 1.5 ×, of the 6th flagellomere 1.2 ×, and of the 7th flagellomere 1.5 × its length, respectively (Fig. 6H).

Mesosoma. Mesoscutum transverse, width 2.0 × its length; notauli incomplete, not adjacent to transscutal articulation; scutoscutellar sulci converge medially, not adjacent to transscutal articulation; mesometapleuron with longitudinal striations in ventral two thirds, smooth in dorsal one third; lateral propodeal projections thin and long and oriented posteriorly, translucent and amber-coloured; median propodeal projection overhangs the anterior margin of the metasoma with its apical half.

Legs. Metafemur distinctly thickened, length more than 2.0 × its width.

Metasoma. Six basal longitudinal carinae on the syntergite; anterolateral syntergite with row of setae.

Male. Unknown.

Host. Unknown.

Distribution. Oriental (Vietnam).

Remarks. This reinterpreted description is based on a transliteration of the original description, with terminology clarified and standardised, especially for antennal terms. The original description of the antennal segments measurements is ambiguous when compared to the corresponding illustration (Alekseev 2004). It is unclear whether the author refers to the numbering of the flagellomeres or the antennomeres (which include the scape and pedicel) when describing the 4th and 5th segments as being approximately equal in length and width, and the 6th–8th segments as being transverse. In reinterpreted description, we refer to the corresponding flagellomeres, maintaining the originally determined ratios but revising the numbering of the flagellomeres to align with the redescription and the illustration. The type specimen was not found (pers. comm. Belokobylskij S.A.), so no images were taken, and no re-examination was conducted.

Discussion

A closer look at the allegedly monotonous genus *Ceraphron* shows that the genus has quite heterogeneous species, justifying a subdivision into subgenera. Currently, six subgenera are defined, and we have prepared a checklist of all known species within these subgenera, along with their depositories, except for the subgenus *Ceraphron* (Table 1). Since the type species of the genus *Ceraphron*, *C. sulcatus* Jurine, 1807, is destroyed and only known from a drawing of the habitus and antenna, the nominal subgenus *Ceraphron* (*Ceraphron*) cannot be accurately defined (Dessart 1978, 1981). The designation of a neotype should be made later. In principle, any species that cannot be confidently attributed to one of the five aforementioned subgenera is by default placed in the nominal subgenus *Ceraphron* (*Ceraphron*). As a result, *Ceraphron* (*Ceraphron*) acts as a so-called "garbage can" subgenus for species that lack clear subgeneric placement, highlighting the necessity of a thorough taxonomic revision.

Table 1. List of all known subgenera and species of the genus *Ceraphron* Jurine, except for the subgenus *Ceraphron*. AFR – Afrotropical (sometimes referred to as Afrotropics) AUS – Australasian; NEA – Nearctic; NEO – Neotropical (sometimes referred to as Neotropics); OTL – Oriental; PAL – Palaearctic.

Subgenus	Species name	Author(s)	Depository	Distribution
Allomicrops	*C.* (*A.*) *abnormis*	Perkins, 1910	BPBM	AUS, NEA
	C. (*A.*) *barbieri*	Dessart, 1975c	ZMUC	NEA, PAL
	C. (*A.*) *bispinosus*	(Nees von Esenbeck, 1834)	?	NEA, PAL
	C. (*A.*) *masneri*	Dessart, 1963	RBINS	AFR
	C. (*A.*) *saxatilis*	Kieffer, 1912	NHMUK	AFR
	C. (*A.*) *stenopterus*	(Dessart, 1965)	MCSN	PAL
Ceraphron	> 200 spp.	—	—	AFR, AUS, NEA, NEO, OTL, PAL
Eulagynodes	*C.* (*E.*) *aguinaldoi*	Dessart, 1981	USNM	OTL
	C. (*E.*) *caccabatus*	Dessart, 1981	RBINS	OTL
	C. (*E.*) *dichromus*	Dessart, 1981	USNM	OTL
	C. (*E.*) *laticornis*	Alekseev, 1994	ZIN	OTL
	C. (*E.*) *notauliciferus*	Dessart, 1975a	MHNG	OTL
	C. (*E.*) *splendens*	Dessart & Alekseev, 1982	ZMUM	PAL
	C. (*E.*) *svetlanae*	Alekseev, 1995	ZIN	PAL
	C. (*E.*) *triochros*	Dessart, 1975a	RMCA	AFR
	C. (*E.*) *variolosus*	Dessart, 1975a	RMCA	AFR
Larsoceraphron	*C.* (*L.*) *chularoipaad*	Ghafouri Moghaddam, Salden & Butcher, 2025	CUMZ	OTL
	C. (*L.*) *huggerti*	Dessart, 1981	RBINS	OTL
	C. (*L.*) *sylviae*	Dessart, 1981	CNC	NEO
	C. (*L.*) *tobiasi*	Alekseev, 2004	ZIN	OTL
Oktoceraphron	*C.* (*O.*) *bessalis*	Dessart, 1975b	CNC	NEO
Pristomicrops	*C.* (*P.*) *depressus*	Dessart, 1975a	MHNG	OTL
	C. (*P.*) *planus*	Dessart, 1990	ANIC	AUS
	C. (*P.*) *pristomicrops*	Dessart, 1965	MCSN	PAL
	C. (*P.*) *punctatellus*	Dessart, 1990	RBINS	AFR
	C. (*P.*) *vegrandis*	Dessart, 1990	RBINS	AFR
	C. (*P.*) *ypsilon*	Dessart, 1996	RBINS	PAL

The recorded host range of *Ceraphron* encompasses at least 12 families across four insect orders (Table 2; Moser et al. 2024). Their parasitisation strategies include both endoparasitism and ectoparasitism, as well as solitary and gregarious development. Some ceraphronoids are also known to be hyperparasitoids. The limited available data suggest that members of Cecidomyiidae and Formicidae serve as the primary hosts or associates (Moser et al. 2024). However, it is important to note that most described species lack recorded host data, and the actual variety of hosts is likely much higher. Additionally, the validity of some host records remains uncertain and requires further confirmation, which will be crucial for future studies. Despite the importance of host associations, less attention has been given to studying and rearing ceraphronids compared to the extensive efforts dedicated to collecting them for DNA barcoding and taxonomic research using various trapping methods. As a result, our current knowledge remains limited, over 80% of known ceraphronoid wasp species lack documented host associations, and among the available records, some are questionable. Considerable

Table 2. Host records of known subgenera of *Ceraphron* Jurine.

Subgenus	Host Orders	References
Allomicrops	Diptera (Cecidomyiidae), Hymenoptera (Dryinidae, Formicidae)	Swezey 1908; Kieffer 1914; Dessart 1963, 1981; Jansen and Chavalle 2014
Ceraphron	Diptera (Agromyzidae, Cecidomyiidae, Sciaridae), Hemiptera (Coccidae, Homotomidae), Hymenoptera (Braconidae, Formicidae, Pteromalidae)	Ratzeburg 1852; Rondani 1877; Kieffer 1914; Ishii 1938; Risbec 1953; Dessart 1962; Laborius 1972; Dessart 1989; Jansen and Chavalle 2014; Moser et al. 2024
Eulagynodes	Lepidoptera (Gracillariidae)	Girault 1917; Dessart 1981
Larsoceraphron	Unknown	Dessart 1981
Oktoceraphron	Unknown	Dessart 1975b; Dessart and Cancemi 1986
Pristomicrops	Unknown	Dessart 1981

effort will be required to obtain a more comprehensive and accurate understanding of host-parasitoid relationships in *Ceraphron* species.

The recently described species *Ceraphron krogmanni* Ulmer, Mikó & Deans, 2018 is similar to the subgenus *Larsoceraphron* by having distinct ocellar foveae, incomplete notauli, and an epomial carina (as seen in *Trassedia* and megaspilid wasps). However, it lacks several key characters of *Larsoceraphron*, including a distinct posteriorly protruding occipital carina and a distinctly more prominent internotaular area relative to the scapula (Ulmer et al. 2018). These morphological differences suggest that *C. krogmanni* may not fully conform to the diagnostic traits of any currently recognised subgenus within *Ceraphron*. Sequencing of multiple genetic markers would allow for a robust comparison with other subgenera within *Ceraphron*. Such data would provide insights into whether the observed morphological intermediacy reflects shared ancestry, evolutionary convergence, or an independent lineage. Additionally, integrating molecular data with detailed morphological studies could improve the taxonomic resolution and lead to a more accurate understanding of the evolutionary history of the severely neglected genus *Ceraphron*.

The type species of the subgenus *Larsoceraphron* was originally described from Brazil (Neotropical region), while other described species are from the Oriental region. This disjunct distribution, spanning both the Old and New World tropics, raises important biogeographical and evolutionary questions. Although all species occur in tropical climates, their geographic separation suggests either a historical connection or independent dispersal events. Several possible explanations could account for this pattern.

The substantial geographic gap between known populations highlights the need for a thorough taxonomic revision to confirm species validity and phylogenetic relationships. Cryptic diversity may exist within both *Ceraphron* and *Larsoceraphron*, and some currently recognised species could represent distinct, undescribed lineages. To resolve these uncertainties, future studies should integrate molecular phylogenetics, detailed morphological analysis, and ecological data to clarify the evolutionary history and biogeographic patterns of *Larsoceraphron*.

Currently, DNA barcode data are available in BOLD Systems (http://www.boldsystems.org, accessed 23/02/2025), with at least 430 published records containing

sequences that form 166 BINs (=166 putative species clusters) for the family Ceraphronidae from Thailand in the public dataset. For the family Megaspilidae, there are 58 published records with sequences forming 19 BINs. In contrast, Butcher and Quicke (2023) reported that there are approximately 20 species of *Ceraphron*, ten of *Aphanogmus*, and one or two of *Cyoceraphron* Dessart 1975 in Southeast Asia. Additionally, Megaspilidae is represented by fewer than ten species of *Lagynodes* Förster, 1840 (see also Dessart, 1999), approximately ten of *Conostigmus* Dahlbom, 1858, and a few more of *Dendrocerus* Ratzeburg 1852 in the region. All of these genera are cosmopolitan, with the vast majority of described species originating from the Palaearctic and Nearctic regions (Butcher and Quicke 2023).

Interestingly, the markedly higher number of BINs observed for Ceraphronidae (166) compared to Megaspilidae (19) may reflect a genuine difference in species richness between the two families in Thailand. While some degree of sampling or identification bias cannot be ruled out, the disparity likely reflects true differences in diversity. Moreover, the discrepancy between the number of BINs recorded in Thailand and the reported number of species in Southeast Asia highlights a striking taxonomic gap. With 166 BINs for Ceraphronidae in Thailand alone, far exceeding the stated 30 species for the entire region, it is evident that a vast number of species remain undescribed. Similarly, the presence of 19 BINs for Megaspilidae in Thailand suggests a significantly higher species richness than previously recognised for Southeast Asia. These findings underscores that both Ceraphronidae and Megaspilidae are grossly understudied. The current records from Thailand alone already hint at a vastly richer fauna, yet formal taxonomic studies remain minimal. Essentially, these families are still largely neglected in Thailand and, more broadly, across Southeast Asian countries, highlighting an urgent need for systematic research and species description efforts.

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